THE SEASONAL OCCURRENCE OF MYTILUS EDULIS ON THE CAROLINA COAST AS A RESULT OF TRANSPORT AROUND CAPE HATTERAS [1]

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The edible mussel, *Mytilus edulis* L., attaches to rocks, pilings, and other firm substrates, being particularly abundant in the lower intertidal zone, where it is a dominant organism in the community (Newcombe, 1935; Dexter, 1947). A temporate and boreal species, it is found on both American and European coasts of the North Atlantic as well as Asian and American coasts of the North Pacific Ocean. Its distribution has aroused the interest of ecologists as an example of the effects of temperature on determining the geographical limits of species. Hutchins (1947) has suggested that the southern limit of *M. edulis* occurs where the mean sea surface temperature during the warmest month is approximately 80° F. (26.6° C.).

In the western Atlantic, *M. edulis* reaches its southern limit in the Carolinas. Although Hutchins showed the 80° summer isotherm intersecting the coast in the vicinity of Cape Hatteras, the edible mussel has been reported as far south as Charleston, South Carolina, three hundred miles below Cape Hatteras. This apparent contradiction of Hutchins' temperature limitation of *M. edulis* is discussed and related to the biology of the species. Its occurrence on the North Carolina coast is analyzed in relation to coastal water masses, their temperature and movement, and meteorological conditions.

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Observations

Mytilus edulis has been collected in the course of study of littoral organisms in the Beaufort and Cape Hatteras areas (Fig. 1). In the latter region, this study has centered on fauna attached to a group of eight wrecks near the outer beach. All but one wreck ordinarily extend above the water surface; all are metal and provide a firm substrate for many sessile organisms. *Mytilus edulis* occurs all year long on wrecks north of Cape Hatteras (stations 1–6: Kitty Hawk, Overlook, Pea Island, Rodanthe, Waves, and Salvo), where it is the dominant organism in the lower part of the intertidal zone and extends into deeper water on subtidal surfaces.

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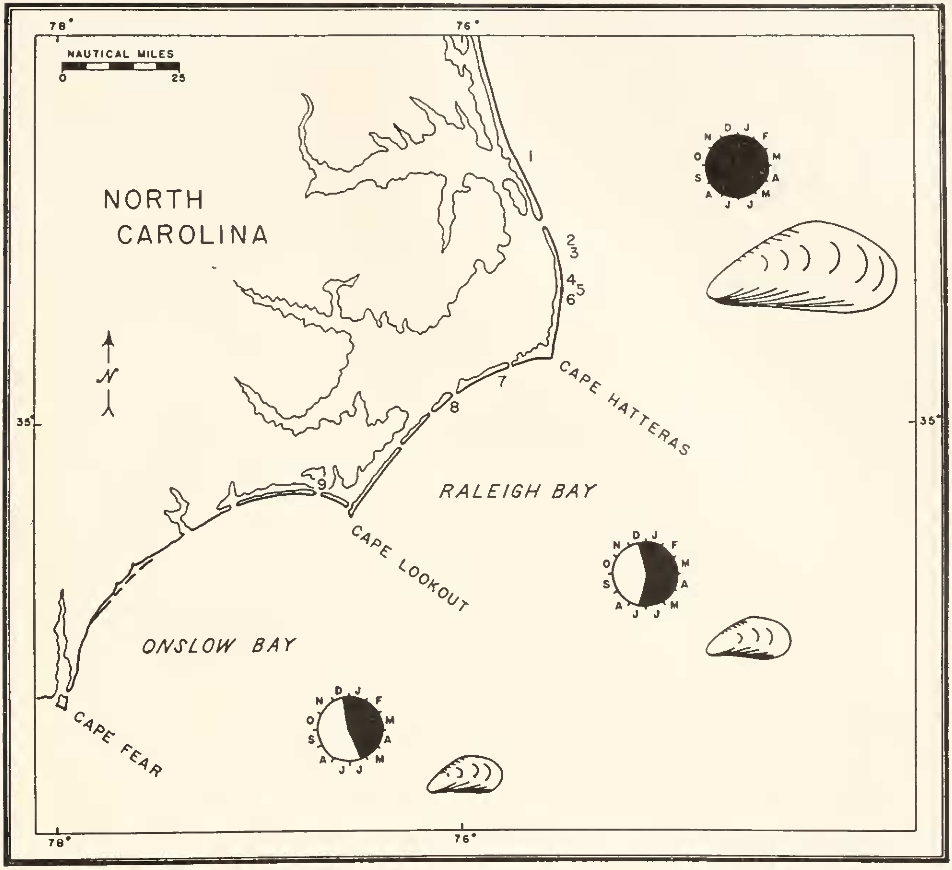

FIGURE 1. Chart of North Carolina coast, showing stations for the collection of *Mytilus edulis,* the portion of the year that *M. edulis* is present in each region, and the relative size attained by this species in each region. The blackened portion of the clock symbol indicates the presence of *M. edulis.* Station 1—Kitty Hawk, 2—Overlook, 3—Pea Island, 4—Rodanthe, 5—Waves, 6—Salvo, 7—Ocracoke Island, 8—Portsmouth Island, 9—Beaufort.

Here, it attains a maximum size of at least 75 mm. However, on the two wrecks in Raleigh Bay, south of Cape Hatteras (Ocracoke and Portsmouth, stations 7 and 8), *M. edulis* has been found only in spring, disappearing in late July. The maximum size attained in Raleigh Bay is 33 mm.

In the Beaufort area (station 9), *M. edulis* has been collected on rock jetties and pilings near Beaufort Inlet, where it shares its intertidal habitat with *Brachidontes exustus,* a small ribbed mussel which is distributed from North Carolina to the West Indies. Variable in abundance from year to year, *M. edulis* in the Beaufort area is often relatively scarce, with a few individuals scattered among large populations of *B. exustus.* Occasionally, however, it is very abundant in the spring, far outnumbering *Brachidontes.* While adequate records over a long period of time have not been kept, it is known that the appearance of *M. edulis*

in large numbers occurs at irregular intervals. It was very abundant in June, 1938; Stephenson and Stephenson (1952) noted that it was common locally in April and May, 1947; and there have been several years in the past decade when it has been abundant in the spring. *M. edulis* appears during the winter months. Ordinarily it disappears in June, leaving *B. exustus* as the predominant mussel on pilings and jetties in the intertidal zone. In the Beaufort area, *M. edulis* is small, attaining a maximum size of only 30 mm.

While *M. edulis* is a permanent resident and a dominant organism of the intertidal zone north of Cape Hatteras, the niche it occupies is largely taken south of the Cape by *B. exustus*.

Discussion

Temperature

The differential success of *M. edulis* on the North Carolina coast can be attributed to differences in water temperatures. Two distinct types of water lie off the coast, exhibiting different temperature and salinity characteristics. These have been designated (Bumpus and Pierce, 1955) as Virginian Coastal water, extending northward from Cape Hatteras to Cape Cod, and Carolinian Coastal water, extending southward from Cape Hatteras to Cape Canaveral. Virginian Coastal water is much colder than that of the more southern Carolinian Coastal water (Fig. 2). At Cape Hatteras, there is typically a sharp temperature gradient (Parr, 1933), and these water types remain relatively distinct, with little mixing.

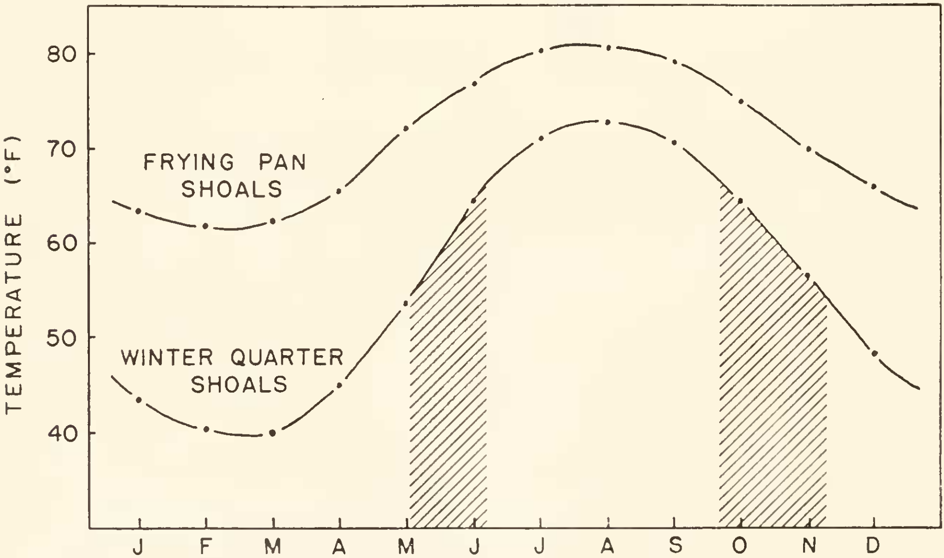

FIGURE 2. Monthly means of sea surface temperature at Frying Pan Shoals Lightship (Carolinian Coastal water) and Winter Quarter Shoals Lightship (Virginian Coastal water). Shading indicates periods of temperature suitable for attachment of *Mytilus edulis* in the southern part of Virginian subprovince. Data for 1947–1956 for Frying Pan Shoals and 1925–1940 for Winter Quarter Shoals from Bumpus (1957a).

Biologically, these temperature conditions are extremely important, determining which species survive along each part of the coastline. The temperature gradient in the Cape Hatteras area helps to separate the fauna of the Virginian biogeographic subprovince from that of the Carolinian subprovince. On the basis of their respective temperature regimes, the Virginian subprovince can be classified as a temperate zone (8–25° C., 46–77° F.), and the Carolinian subprovince can be classified as a sub-tropical zone (15 to almost 30° C., 59–85° F.) in the classification system of Vaughan (1940).

South of Cape Hatteras, summertime maximum temperatures may exceed the thermal limits of *Mytilus edulis*. Ritchie (1927) found that this species was killed by a fourteen-hour exposure to 84° F., and Bruce (1926) has indicated that it could not survive more than one hour at 86° F. We have recorded water temperatures as high as 84° F. along the shore of Raleigh Bay in August, 1959, and Maturo (1959) recorded a similar temperature in the Beaufort area in August, 1954. These are not temperatures of estuarine water that had warmed over shallow inshore areas; they represent oceanic conditions to which mussel populations would be exposed. These summertime temperatures are sufficiently high to cause the death of any edible mussels south of Cape Hatteras. Death in nature may precede the attainment of the high temperatures cited.

The annual date of disappearance from the natural habitat is advanced or delayed in relation to the progression of the temperature cycle. For example, in the spring of 1956 when mean air temperatures in eastern North Carolina were several degrees lower than average (U. S. Weather Bureau, 1956), and water temperatures along the middle Atlantic Coast were similarly depressed (Bumpus, 1957b), the delay in vernal warming permitted *Mytilus edulis* and many other organisms of the winter sequence to persist in the Beaufort area well into July. In the Beaufort area, the disappearance of mussels more closely coincides with the attainment of a water temperature of 80° F. It seems likely that higher air temperatures and solar radiation raise the temperature of mussels to a critical level during their exposure at low tides. Under these conditions, the 80° isotherm chosen by Hutchins to represent the southern limit of *M. edulis* serves better than 84° as an empirical expression of the ecological requirements of this species. The different dates of disappearance recorded for the Beaufort area (mid-June) and for the Ocracoke area (late July) reflect a later date for the attainment of lethal high temperatures in the more northern Ocracoke area.

North of Cape Hatteras, such high temperatures do not occur in the ocean, and *M. edulis* survives the maximum temperatures of summer. Just as an upwelling of cool bottom water permits *M. edulis* to live on the coast of Lower California, Mexico (Woods Hole Oceanographic Institution, 1952), an upwelling of cool subsurface water contributes to the maintenance of a suitable environment for this species north of Cape Hatteras (Wells and Gray, 1960). The occurrence of this cooler water north of the Cape permits the maintenance of sizable populations of other northern species with boreal affinities (Wells *et al.*, 1960).

Water movements

In view of the fact that Carolinian Coastal water is too warm to permit year-round survival south of Cape Hatteras, *Mytilus edulis* in this region must owe its

existence to larvae originating from the extensive populations north of the Cape, which could renew colonies south of the Cape, if they were provided suitable transport. However, while it is recognized that a southward-flowing coastal current follows the edge of the continental shelf off the middle Atlantic Coast, this coastal current normally does not pass Cape Hatteras; instead, it turns seaward and parallels the Gulf Stream, flowing in a northeasterly direction (Bigelow, 1933; Ford *et al.,* 1952). The Gulf Stream System approaches Cape Hatteras from the south and then flows northeastward, away from the North American mainland (Iselin, 1936). Because the Outer Banks of North Carolina project across much of the continental shelf, the average position of the inner edge of the Gulf Stream lies only ten miles off the point of Cape Hatteras (Marshall, 1951), and the Gulf Stream System has a marked effect on this part of the coastline. As a result of the convergence of these two currents on the Cape Hatteras region, there is a pronounced offshore movement of water. Bumpus (1955) noted the offshore movement of several drift bottles released in 1950 in the Cape region. Such conditions would appear to bar the movement of mussel larvae around Cape Hatteras; instead, the larvae would be carried out to sea.

Although there is no regular movement of water around the Cape, Bumpus and Pierce (1955) witnessed the breaching of this barrier and postulated the sporadic occurrence of transient indrafts of Virginian Coastal water into Raleigh Bay, as the result of northeast storms in the Cape Hatteras region. The duration of a northeast storm and the subsequent weather pattern apparently would determine the fate of this parcel of Virginian Coastal water. If the storm lasts but one or two days, this water may eventually be absorbed within the Carolinian Coastal water by mixing, or a violent meander of the Gulf Stream may sweep over the continental shelf, pushing or drawing the Virginian Coastal water to the northeast. If the northeast storm persists or is followed closely by another northeast storm, the parcel of Virginian Coastal water may grow in size and be driven farther southward, around Cape Lookout into Onslow Bay. Northeast storms, common in fall and winter months, are a characteristic component of the climate on this coast. Strong northeasterly winds push water southward past the point of Cape Hatteras. By the mechanism described by Chase (1959) concerning the effect of wind on water movement, wind tides produced north of the Cape help to move Virginian Coastal water across Diamond Shoals.

Bumpus and Pierce (1955) found Virginian Coastal water in Raleigh Bay in January, 1954, after a three-day storm. A similar parcel of water with the characteristics of Virginian Coastal water was noted at Frying Pan Shoals Lightship in November, 1956, following an extended period of northeast storms in the Hatteras area (Bumpus, 1957b). Again, for April, 1958, Day (1960) recorded the occurrence of Virginian Coastal water at Frying Pan Shoals, 145 miles southwest of Cape Hatteras. Bumpus (1957b) noted that this southward movement of water had progressed at the rate of seven or eight miles per day. At the height of a storm, water has been observed flowing past the point of Cape Hatteras at a rate of one to two knots. After having paralleled the coastline north of the Cape, it continues to flow in a southward direction rather than following the coast westward.

Bumpus and Pierce suggested that this southward movement of water might distribute northern planktonic elements southward along the coast, and that this might account for the presence of anomalous species of northern affinities in the winter-spring sequence in Onslow Bay. Both Williams (1948, 1949) and Sutcliffe (1950) had found a number of northern species in this area whose occurrence was apparently restricted to the cold months of the year. *Mytilus edulis* appears to be such an anomalous species in the Carolinian subprovince. Larvae of this species from north of Cape Hatteras could be distributed along the coast south of the Cape by such a water movement.

Settlement period

To be effective in the transport of *Mytilus edulis* larvae, these storms must occur during the reproductive period of the mussel. The period of breeding and attachment of this species occurs at different times in different parts of its range, apparently in response to temperature conditions. Engle and Loosanoff (1944)

TABLE I

Attachment of Mytilus edulis *at various locations*

Locality	Beginning		Maximum		Reference
	Date	Temp. (° C.)	Date	Temp. (° C.)	
Lamoine, Me.	June (late)	13	July (end)	15	Fuller, 1946
Milford, Conn.	June 1	12	June 15	15	Engle and Loosanoff, 1944
Oakland, Calif.	March	14	May	18	Graham and Gay, 1945
Kola Fjord, USSR	July	12	—	—	Zenkevitch, 1935
Millport and Caernarvon, U.K.	July	12	—	—	Bengough and Shepheard, 1943
Plymouth, U.K.	June	13	—	—	Mott, 1944
Kanazawa, Japan	January	10	May	17	Miyazaki, 1938

found *M. edulis* settling in early June at Milford, Connecticut, when the water temperature was 12.5° C. (about 54° F.). Attachment reached a peak about a month later, then fell off when water temperatures reached 19° C. (66° F.). After a brief halt in the first half of August, some attachment occurred in late August, when water temperatures were declining from the seasonal maximum. A comparison of the dates of attachment from other studies (Table I) shows that attachment typically follows the pattern observed at Milford, beginning near 12° C. (54° F.) and reaching a maximum at 15 to 18° C. (59–64° F.).

In the southern part of the Virginian subprovince, there appear to be two important periods of settlement of *Mytilus* larvae, one in late spring and one in late fall, well separated by a warm period when little or no settling occurs. Spring attachment may begin in April, when water temperatures warm to about 54° F., and extend into early June. Optimum conditions are again realized in October and November, when water temperatures are between 66 and 54° F. These temperature intervals are interposed on the graph of water temperatures at Winter

Quarter Lightship in Figure 2. Evidently, the late fall attachment period is more important than the late spring attachment period for colonizing the northern part of the Carolinian subprovince. Northeast storms are more likely in the October-November period than in late spring, and mussels which attach in May are soon killed by high temperatures south of the Cape. Only the late fall set would have the opportunity to grow to sizable dimensions. *Mytilus edulis* has been noted in the Beaufort area starting in December with representatives of the fall set. Only representatives of this set could reach a length of 30 mm. by the time the summer mortality sets in. Therefore, northeast storms in fall months should be primarily responsible for the appearance of mussel populations south of Cape Hatteras.

Correlation with weather records

From the above discussion, it would appear that the occurrence of *Mytilus edulis* south of Cape Hatteras can be directly related to movements of water around the Cape resulting from northeast storms. However, to be effective these storms must occur during the fall reproductive period for this species. An examination of the cycle of monthly mean water temperatures shows that this period ordinarily occurs in October and November (Fig. 2), but warmer than average conditions in September will extend the attachment period into December, and cooler than average conditions in September will make the latter part of that month suitable

TABLE II

Northeast storms in the Cape Hatteras area suitable for the transport of Mytilus edulis *larvae south of Cape Hatteras, 1954 to 1958, with relative abundance of* Mytilus edulis *at Beaufort the following spring*

	Number of days	Dates	Mean wind velocity (mph)	*Mytilus edulis*
1954	—	none	—	none
1955	3	October 2–4	14.0	rare
1956	7	October 10–16	17.7*	
	3	October 19–21	14.5	
	6	October 24–29	20.4*	abundant
	5	November 2–6	15.3	
	—			
	21			
1957	3	October 3–5	10.8	moderately
	5	October 11–15	13.0	abundant
	—			
	8			
1958	4	October 6–9	16.9	
	4	October 18–21	10.6*	abundant
	—			

* Severe storm; tides 2 to 3 feet above normal.

for attachment. Bumpus and Pierce noted that a short-lived storm is not effective in causing a significant penetration of water south of Cape Hatteras, and suggested that a storm that lasted for three days or more was necessary to produce the southward movement. With these criteria in mind, weather records for Cape Hatteras (Local Climatological Data) have been examined for the occurrence of northeast storms during the five-year period from 1954 to 1958. Only those storms were counted in which a northeasterly wind (NNE, NE, or ENE) predominated three or more days, with a mean velocity in excess of 10 mph. Using water temperature records by Bumpus (1957a, 1957b) and Day (1958, 1960) as a guide to the late fall attachment period of *M. edulis,* the northeast storms which could have carried mussel larvae south of Cape Hatteras during this five-year period are listed (Table II).

Mean wind velocity is included in Table II as a measure of the likely effectiveness of each storm in moving Virginian Coastal water southward. While 1958 storms extended over as many days as 1957 storms, a greater severity and effectiveness of the 1958 storms is indicated by a greater wind velocity. The fall of 1956 was distinguished by a remarkable series of storms in October and early November, with only brief intermissions. It was after these storms in 1956 that a parcel of Virginian Coastal water was detected off Frying Pan Shoals.

Relative abundance of *Mytilus edulis* at Beaufort the following June is also included in Table II. Although *M. edulis* may comprise up to 80% of the mussels on the jetties and pilings, such populations are uncommon. Ordinarily, it comprises less than 10% of the mussels, the great majority being *Brachidontes exustus.* If *Mytilus edulis* colonies in the Beaufort area owe their existence to a transport of larvae around Cape Hatteras by northeast storms the preceding fall, a close correlation would be expected between the number and severity of northeast storms and the abundance of *M. edulis* at Beaufort the following June. A comparison of these items in Table II shows a very close correlation. Not only does the occurrence of *M. edulis* agree quantitatively with the prior occurrence of northeast storms, but this species was not found in the spring following an exceptionally storm-free fall season in 1954. The greatest abundance of mussels was recorded after the remarkably stormy fall of 1956. The abundance of mussels also reflected the relative severity of storms in the fall of 1957 and 1958, mussels being more common after the 1958 season. It seems evident that this is a cause-effect relationship.

The presence of *Mytilus edulis* in the northern part of the Carolinian subprovince serves as an indication of the southward penetration of Virginian Coastal water. Consequently, the presence of *M. edulis* at Charleston, South Carolina, indicates that Virginian Coastal water may be driven this far south.

Other species

Other molluscs of northern affinities probably owe their sporadic appearance in the Beaufort area to a similar transport of their larvae southward around Cape Hatteras by northeast storms. For example, although the normal range of *Littorina saxatilis* in the western Atlantic extends from the Arctic to Cape May, New Jersey (Abbott, 1954), Stephenson and Stephenson (1952) reported that species in the Beaufort area during April and May, 1947. The anomalous appear-

ance in the Beaufort area suggests that it, too, was transported southward around Cape Hatteras in larval stages. At Cape Ann, Massachusetts, Dexter (1947) noted spectacular fluctuations in abundance of *L. saxatilis* for year to year in the same location. Such variation in numbers indicates that larvae of this species are subject to water movements, and that they may be carried some distance from the parent colony. Its appearance in Beaufort would be in keeping with this type of distribution.

Summary

Although *Mytilus edulis* survives year-round north of Cape Hatteras, summer water temperatures are high enough to kill it south of that point. Populations of this species in the Carolinian subprovince are apparently maintained by an external source of larvae. Larvae can be transported around Cape Hatteras by southward movements of Virginian Coastal water that result from persistent strong northeast winds in late fall. The presence and abundance of *M. edulis* at Beaufort has been correlated with the abundance and severity of northeast storms occurring in the Cape Hatteras region during the preceding fall, over a five-year period. Probably other northern species owe their sporadic appearance in the Beaufort area to similar transport of larvae by southward water movements.

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